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Niche separation by mink and river otters: coexistence in a marine environment

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We studied habitat selection and niche separation by mink (*Mustela vison*) and sympatric river otters (*Lutra canadensis*) living in a coastal environment in Prince William Sound, Alaska, during summer 1991. We hypothesized that exposure to wave action, depth of tidal zone, substrate composition, and availability of cover were important habitat variables in selection of sites by mink at the terrestrial – marine interface. We also hypothesized that because of high resource abundance, little resource partitioning would occur between mink and river otters in the marine environment, leading to a large niche overlap. We employed step-wise logistic regression to develop a model separating feeding sites of mink, based on trails and latrines, from random sites. This model identified vegetated slope, tidal slope, overstory (old-growth forest), understory (brush), small rocks, and exposure to wave action as the variables characterizing sites selected by mink. Mink selected (use > availability) shallow vegetated slopes and tidal slopes. Mink also selected sites that were more protected from wave action and with more overstory cover, but avoided (use < availability) beaches with small rocks as the main substrate, which is likely to be correlated with low availability of food. Analysis of niche overlap identified exposure and overstory as two variables that differ significantly between these two mustelids. Niche overlap including all habitat variables was 48%. Removal of exposure and overstory from this calculation resulted in 78.5% overlap. River otters selected sites with high exposure to wave action, whereas mink selected sites with low and medium exposure. Otters selected sites with high overstory cover, whereas mink showed less preference for such sites. Therefore, we have recorded niche separation in a marine environment, but were unable to attribute it to competition. Moreover, pronounced resource partitioning occurred even when food was abundant.

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Studies of diets of mink (*Mustela vison* Schreber) living in marine environments have shown the importance of intertidal prey (Johnson 1985, Dunstone and Birks 1987, Dunstone 1993). In those studies, intertidal fish and invertebrates were the main foods of mink. Although mink forage under water and sometimes hunt while diving, the relatively small surface area of their feet, their anterior propulsion, and their low storage capacity for O₂ make mink inefficient

swimmers compared with other diving mammals (Dunstone and O'Conner 1979a,b, Williams 1983, 1989, Williams and Kooyman 1985, Stephenson et al. 1988). This limitation on swimming and diving efficiency affects duration and depth of dives especially in sea water, which has higher density and viscosity than fresh water (Vogel 1981). Selection of feeding sites by mink is related to features of its habitat that will affect its foraging success (Dunstone 1978). We tested which

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habitat variables were most important to foraging mink in a coastal environment, and hypothesized that exposure to wave action, depth of tidal zone, substrate composition, and availability of cover were the important habitat variables in selection of sites by mink at the terrestrial-marine interface.

River otters (*Lutra canadensis* Schreber) inhabiting marine environments occur sympatrically with mink, and forage in the intertidal and subtidal zones for marine fish and invertebrates. (Larsen 1984, Stenson et al. 1984, Woolington 1984, Bowyer et al. 1994). Although better equipped for swimming and diving (Fish 1994), river otters forage close to shore in the vicinity of their latrine sites (pers. obs.; for *Lutra lutra* see Kruuk et al. 1990). Several studies in fresh-water systems have shown that although mink and river otters (*L. canadensis* in North America; *L. lutra* in Europe) coexist in a variety of habitats, exploitation and interference competition can occur between these two predators on a seasonal basis, especially when food availability is reduced and alternative prey are not readily available (Erlinge 1972, Melquist et al. 1981, Wise et al. 1981, Humphrey and Zinn 1982). Inter- and subtidal zones in the Gulf of Alaska have high species diversity and high biomass of invertebrates and fish (Feder and Jewett 1986, O'Clair and Zimmerman 1986, Rogers et al. 1986). Competition leading to resource partitioning and reduced niche overlap will occur when resources are limited (Glasser and Price 1988; see Keddy 1989 for review). We hypothesized that little resource partitioning and niche separation would occur between mink and river otters in Prince William Sound, Alaska, because of the apparent superabundance of prey (Feder and Jewett 1986, O'Clair and Zimmerman 1986, Rogers et al. 1986).

Methods

Study area

Prince William Sound is located in south-central Alaska, USA (Fig. 1), and has a maritime climate; summers are cool and wet and winters are characterized by deep snow (2200 mm annual precipitation). High elevations are typified by alpine tundra, and low elevations by old-growth forest (primarily *Tsuga heterophylla* and *Picea sitchensis*) with a well-developed understory (mainly *Vaccinium*, *Menziesia*, and *Rubus*). Alder (*Alnus*) tends to occur on disturbed sites, and near the boundary of terrestrial vegetation and the intertidal zone. Shorelines are steep and rocky with numerous inlets, bays, and coves.

Sampling

Three mink (2 females and 1 male) were live captured in Shoestring cove, (Fig. 1), during the first week of June 1991, using Tomahawk live traps. After immobilization

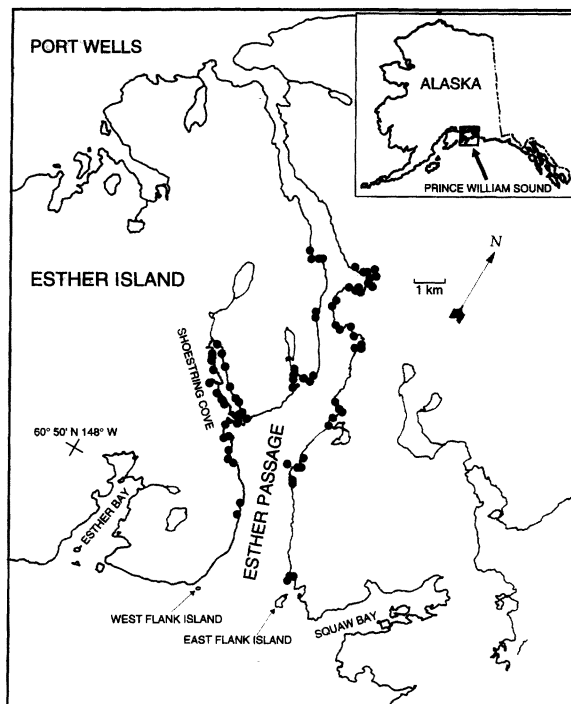


Fig. 1. Location of study area in Esther Passage, Prince William Sound, Alaska. Dots represent mink feeding sites we sampled in 1991; data from river otters are provided by Testa et al. (1994).

with Ketamine (15 mg/kg body mass), we transported them to camp where they were surgically implanted with radio-transmitters (Telonix, Mesa, AZ) by a veterinarian (for similar procedures on river otters see Duffy et al. 1993). After recovery, animals were released near their site of capture. All methods used in this study were approved by an independent Animal Care and Use Committee at the Univ. of Alaska Fairbanks.

Radio-locations were obtained once a day from a small boat or from shore, at random times, every second day from June to mid-August 1991. Activity of mink and tidal level were recorded. From extensive surveys of the shoreline from West Flank Island northward (Fig. 1), we identified 78 feeding sites of mink along both shores of Esther Passage during summer 1991. This area was occupied by at least five mink (three radio-tagged individuals, and two additional ones that were observed occasionally). In this analysis, we avoided using feeding sites directly located by radio-tracking to avoid bias in the results from the small number of radio-telemetered animals. Feeding sites of mink were identified by trails leading to the water. We assumed that such trails were routes to feeding sites because mink usually travel on land (Johnson 1985). A trail was considered as that of mink only when a mink latrine site occurred within 10 m of high tide on that trail. Such sites were areas where mink concentrated their activities based on presence of faeces, tracks, and trails (Johnson 1985). Each site was

Table 1. Feeding site characteristics of mink measured in Esther Passage, Prince William Sound, Alaska, 1991.

Habitat categories	Definitions and methods
Coastline topography	
Aspect	Dominant direction of the shoreline at the point the trail reached the water, as established by with a hand-held compass
Exposure	Subjective evaluation of severity of wave action to which the site could be exposed. Three ranked categories: Exposed, Moderate, Protected
Vegetated slope	Measured with a compass at 5° intervals for the portion of the site above mean high tide.
Tidal slope	Measured with a compass at 5° intervals for the portion of the site below mean high tide
Vegetative cover	
Overstory	Old-growth coniferous forest considered to be in a climax state.
Understory (brush)	Various shrub species
Alder	Alder trees
Intertidal substrate	
Gravel	Gravel-rock material with a diameter of 0.5–10.0 cm.
Small rocks	Rock material with a diameter of 10.0 and 25.0 cm.
Large rocks	Rock material with a diameter between 25.0 cm and 6 m.
Bedrock	Rock material with a diameter greater than 6 m

then characterized with respect to topography, composition of terrestrial vegetation, and composition of intertidal substrates (Table 1). Vegetation and intertidal substrates were assessed for a 10-m arc with its pivotal point at mean high tide. We estimated relative cover of vegetation visually. A rank of 0 was given for any category that composed < 25% of the 10-m arc. More abundant vegetation types were assigned ranks of 1 to 4 (1=25%, 2=50%, 3=75%, and 4=100%) arbitrarily. We used the same method to categorize intertidal substrates. We measured vegetated slopes and tidal slopes, to the nearest 5° with a hand-held compass, from mean high tide to a point 10-m distant landward and seaward, respectively. Aspect of the site was recorded in eight compass directions, and exposure to wave action was ranked into three broad categories from protected (2) to exposed (0). For each site classified as a mink trail, we noted the presence or absence of signs of river otters. Similarly, 180 sites selected at random in Esther Passage (from West Flank Island to Port Wells), and 113 latrine sites of river otters, were sampled using identical methods, during summer 1990 (for full description of otter latrine site identification and sampling see Bowyer et al. 1994, 1995, Testa et al. 1994). For those sites, water depth at 30 m distance from mean high tide was recorded from a boat with a weighted rope (nearest 1 m). Because depth at 30 m was positively correlated with tidal slope (Bowyer et al. 1995), we did not measure this variable at the feeding sites of mink.

Statistical analysis

We employed step-wise logistic regression (BMDP; Dixon 1990) to develop the model best separating feeding sites of mink (coded 1) and random sites (coded 0). We controlled for multicollinearity by eliminating one of any pair of variables with $r > |0.45|$. We examined the fit of the logistic-regression model to

our data using Hosmer-Lemeshow goodness-of-fit test. To determine selection for (use > availability) or against (use < availability) habitat variables, we tested those variables that entered the model using contingency tables (Pearson's χ^2 test $\alpha = 0.05$) for the categorical variables and Mann-Whitney tests for continuous variables (Agresti 1990, Hosmer and Lemeshow 1989). Likewise, we used step-wise logistic regression to identify those variables representing differences in habitat use between mink and river otters. We applied the same rules to this procedure as to the one described previously.

To calculate niche overlap we used Schoener's (1968) index:

$$C(ih) = 1 - 1/2 \sum |P(ij) - P(hj)|,$$

where $P(ij)$ represents the proportion of observations for one species (i) and $P(hj)$ the proportion of observation for the second species (h) for a given nonautocorrelated variable (j). We compared the $C(ih)$ value resulting from incorporating all habitat variables, which entered the habitat selection models of each species (for the otter model see Bowyer et al. 1995), to that without the variables identified by the logistic regression model. This procedure allowed us to examine the contribution of these variables to the degree of niche overlap.

Results

Mink selection of feeding sites

The 3 tagged mink (2 females, 1 male) were radio located 37 times (5, 25, 7 times respectively) during summer 1991. These animals were active on 13 occasions, 11 of which occurred during low tide. The other two times mink were active was on an out-going tide. All observations of mink ($n = 6$) we made while measuring

Table 2. Descriptions of shoreline characteristics for mink, river otters and random sites in Esther Passage, Prince William Sound, Alaska.

Habitat characteristic ^a	Mink (n = 78)		Otter ^c (n = 113)		Random (n = 180)	
	mean	SD	mean	SD	mean	SD
Coastline topography						
Aspect (E-W) ^b	0.188	0.683	0.035	0.689	0.001	0.689
Aspect (N-S) ^b	-0.073	0.706	-0.126	0.719	-0.111	0.708
Exposure (0-2)	1.1	0.7	0.6	0.7	0.8	0.7
Vegetated slope ⁽⁰⁾	24.2	10.8	26.8	11.6	37.7	18.0
Tidal slope ⁽⁰⁾	17.4	10.9	18.7	11.3	23.9	15.9
Vegetative cover (ranked 0-4)						
Overstory (old growth)	1.7	0.9	2.3	0.9	1.5	1.2
Understory (brush)	1.7	0.9	1.5	0.8	1.4	1.0
Alder	0.1	0.4	> 0.1	0.2	0.2	0.4
Intertidal substrate						
Gravel	0.7	1.1	0.2	0.7	0.1	0.4
Small rocks	0.4	0.6	0.4	0.7	0.9	1.0
Large rocks	1.2	1.2	0.8	1.1	1.5	1.3
Bedrock	1.8	1.6	2.5	1.6	1.5	1.6

^a Habitat variables are described in Table 1

^b Directional data were sin - cos transformed.

^c From Bowyer et al. 1995.

habitat characteristics occurred during low tides. We were able to observe mink foraging during nine bouts of direct observation; diving was observed once. This latter observation of foraging lasted 45 min. during which the mink performed multiple dives, and pulled its prey, mostly crustaceans, to shore. During the other eight periods of observation, mink were foraging in tidal rockpools.

From the variables described in Table 2, stepwise logistic regression identified those variables most significantly separating feeding sites of mink from ran-

dom sites as: vegetated slope, tidal slope, overstory (old growth), understory (brush), small rocks, and exposure (Table 3). The only variable not introduced to the model was bedrock, which was negatively correlated with large rocks and small rocks ($r > 0.6$). The model correctly classified 85% of all sites to their respective associations [mink feeding site (83%) vs random site (87%)] (BMDP; Dixon 1990). Analysis of the variables that entered this model revealed that mink avoided steep vegetated and tidal slopes, and therefore used slopes that were shallower than avail-

Table 3. Logistic regression model: coefficients, SE and odds ratio for feeding site selection by mink (mink coded 1, random coded 0) and niche separation of mink and otter (mink coded 1, otter coded 0).

$P(y = j) = e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots} / 1 + e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots}$ where j is 0 or 1

Variable			Coefficient	SE	Odds ratio
Mink habitat selection	exposure	(1)	-1.192	0.572	0.304
		(2)	-1.442	0.606	0.237
	overstory	(1)	-0.732	1.06	0.481
		(2)	-3.333	1.09	0.036
		(3)	-1.846	1.15	0.158
		(4)	-4.652	1.66	0.009
	understory	(1)	-1.630	1.03	0.196
		(2)	-2.288	1.10	0.101
		(3)	-2.732	1.25	0.065
		(4)	-4.544	1.85	0.011
	vegetated slope		0.089	0.018	1.09
		(1)	1.555	0.609	4.74
	small rocks	(2)	5.506	1.46	246.0
		(3)	4.810	1.24	123.0
	tidal slope		0.067	0.021	1.07
Otter and mink niche separation	exposure	(1)	-1.057	0.386	0.347
		(2)	-1.420	0.453	0.242
	overstory	(1)	-0.5652	0.858	0.568
		(2)	0.8378	0.793	2.31
		(3)	1.650	0.876	5.21
		(4)	1.174	0.801	3.23

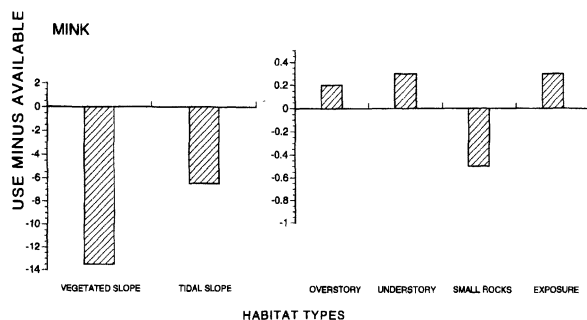


Fig. 2. Use (mink sites) minus availability (random sites) of shoreline habitats, identified by logistic regression analysis. Positive values indicate selection for a habitat feature (use > availability), negative values (use < availability) show avoidance. Selection was significant for vegetated slope ($P < 0.0001$, Mann-Whitney), tidal slope ($P = 0.0018$, Mann-Whitney), small rocks ($P < 0.0001$, χ^2 test, $df = 3$), exposure ($P = 0.0090$, χ^2 test, $df = 2$), and overstory ($P = 0.0001$, χ^2 test, $df = 4$). No significant selection was detected for understory ($P = 0.0986$, χ^2 test, $df = 3$), but in the absence of overstory mink selected sites with significantly higher understory than available ($P = 0.0369$, χ^2 test, $df = 4$).

able. Mink selected sites more protected from wave action and with more overstory cover, but also with more understory shrubs (Fig. 2). Analysis of a multi-way frequency table revealed that in the absence of overstory, mink selected sites that had $\geq 50\%$ understory cover ($P = 0.037$, χ^2 test, $df = 4$), but in the presence of $\geq 25\%$ forest overstory, mink sites did not differ from random sites in selection of understory ($P > 0.3$). Mink strongly avoided shores with small rocks as the main substrate (Fig. 2). Because small rocks were negatively correlated with bedrock, mink likely selected sites with more bedrock. Tidal slope was negatively correlated with the proportional representation of small rock ($r = -0.4$); we interpret this to mean that mink selected shallower slopes with more bedrock.

Resource partitioning by mink and river otters

To evaluate niche overlap of mink and river otters, we introduced the variables measured at sites selected by each species to a stepwise logistic regression procedure with otters coded 0 and mink coded 1 (for the selection model for river otters see Bowyer et al. 1995; means and SD are presented in Table 2). These variables were: vegetated slope, tidal slope, exposure, overstory (old growth), understory (brush), small rocks, and large rocks. The model identified exposure and overstory as two variables that best differentiated habitat use by these two mustelids (Fig. 3, Table 3), and classified 72% of the sites correctly (83% of all otter sites and 53% of all mink sites). Significantly more otter sites were located in $> 50\%$ overstory cover, than were mink sites ($P < 0.0001$, χ^2 test, $df = 4$; Fig. 3). Use of cover by mink did not differ significantly in the

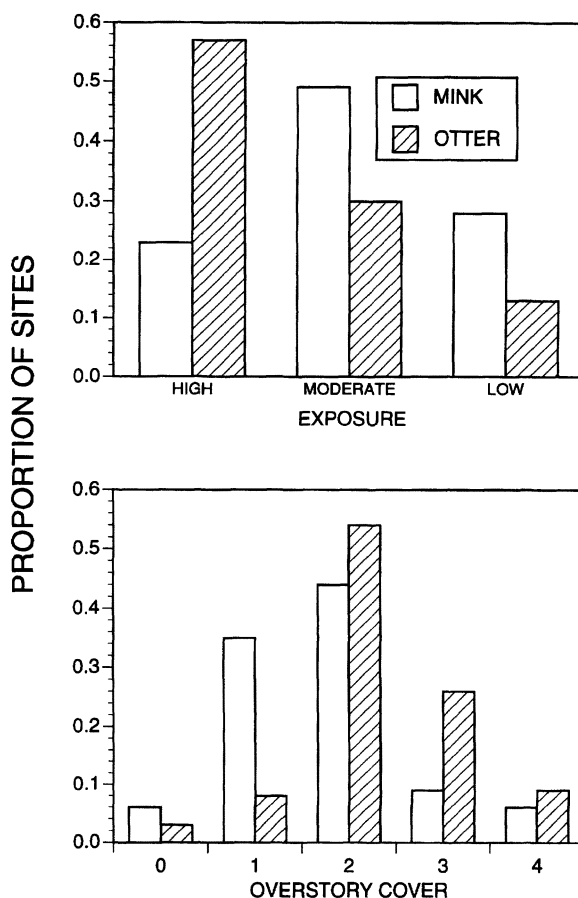


Fig. 3. Use of habitat characteristics by mink (□) and otter (▨) as identified by logistic regression analysis. Mink used more protected sites than did otters ($P < 0.0001$, χ^2 test, $df = 2$), whereas otters used sites with higher overstory cover than did mink ($P < 0.0001$, χ^2 test, $df = 4$).

presence ($n = 51$) or absence ($n = 27$) of otters ($P = 0.25$, χ^2 test, $df = 3$). Otter sites were characterized by high exposure to wave action, whereas, mink sites were characterized by low and medium exposures ($P < 0.0001$, χ^2 test, $df = 2$; Fig. 3). Analysis of use of exposure by mink in low-overstory cover revealed that even in those sites in which otters rarely occurred ($n = 9$), mink significantly used sites with low and medium exposure to wave action ($P = 0.0014$, χ^2 test, $df = 2$).

Schoener's (1968) index, calculated for all variables selected by each of the species, showed a 48% overlap. Removal of exposure and overstory from the calculation resulted in 78.5% overlap, which is a substantial increase in this measure (30.5%). This analysis indicates the importance of these variables in producing resource partitioning by river otters and mink. Records of the absence or presence of otter signs for each mink site revealed that 65% of 78 mink sites had otter signs within the 10-m radius around the site. In many instances (36 of 78) the site used by mink was at the edge of the otter site in higher-density brush; on 12 occasions mink trails led

to the water in a different direction than the trail of otters, resulting in a lower value for exposure.

Discussion

Mink selection of feeding sites

Mink living in a marine environment selected sites that had shallower tidal slopes, were composed largely of bedrock, and were protected from wave action. During low tides, such habitats created more extensive feeding sites for mink, because larger areas of shallow rock-pools were exposed. Johnson (1985) established that high abundance of prey for mink in southeast Alaska was associated with large rocks. Our radio-telemetry data suggested that mink mostly foraged during low tides. Both Johnson (1985) in southeast Alaska, and Hatler (1976) in British Columbia reported similar results. Johnson (1985) reported that mink dove 18% of the time they were foraging and diving occurred during low tide. Hatler (1976) noted diving in 30% of hunting observations he observed for mink, most of which occurred at low tide. Diving during low tide enables mink to reach the shallow subtidal zone, which is characterized by the highest diversity and abundance of crustaceans and nearshore fishes compared with the intertidal or deep subtidal zones (O'Clair and Zimmerman 1986, Rogers et al. 1986). The remainder of observations of hunting by mink were in rock-pools or in eel-grass (*Zostera* sp.) beds exposed by the receding tide (Hatler 1976; pers. obs.). Several intertidal studies in the Gulf of Alaska as well as in other areas have shown that exposed, rocky beaches have a high diversity and biomass of intertidal organisms (Sousa 1979, McGuinness 1987, Feder and Bryson-Schwafel 1988). Mink selection of more sheltered sites (i.e., less productive areas) is likely to be a result of the comparatively low efficiency of swimming by this mustelid. Mink selection for high vegetative cover may be related to exposure to predation by avian predators. Other studies of mink ecology in fresh water as well as in coastal environments detected association with wooded, brushy, or scrubby sites (Gerell 1970, Johnson 1985, Dunstone 1993). Steep vegetated slopes in some areas of Prince William Sound are associated with disturbed sites due to land slides, resulting in low-growing vegetation. Mink selection of shallower vegetated slopes may reflect that phenomenon.

Resource partitioning by mink and river otters

In the separate habitat selection models developed for mink and river otters (Bowyer et al. 1995), similar variables were identified by logistic regression analyses: vegetated slope, tidal slope, exposure, overstory (old growth), understory (brush), small rocks, and large rocks. Inclusion of all these variables in the calculation of the overlap index resulted in low niche similarity for

the two species. The difference between the calculated overlap (48%) and the one obtained by noting presence or absence of otters at mink sites (65%) can be explained by mink sites occurring at the edge of the otter site in higher-density brush. Moreover, in 12 instances mink trails led to water in a different direction than the trail of otters, resulting in a lower value for exposure to wave action. The low overlap value can be interpreted to suggest that resource partitioning occurred between mink and river otters in our study area. Removing exposure and overstory from the overlap calculation resulted in a substantial increase in the niche similarity. Our analysis suggests that mink and river otters selected similar feeding sites (shallow tidal slopes with large rocks). River otters inhabiting shores contaminated by oil spilled from the *Exxon Valdez*, 40 km south of Esther Passage, selected steeper tidal slopes, to avoid oil contamination, than did otters in our study area (Bowyer et al. 1995). Otters from the oiled areas had larger home ranges, less body mass and less diversified diets than those in Esther passage (Duffy et al. 1993, Bowyer et al. 1994), suggesting that sites selected by river otters and mink in our study area are associated with high diversity and high biomass of prey (see also Johnson 1985). A careful examination of the two variables separating sites used by mink and otters reveals that niche separation rather than competitive exclusion occurs in this situation. Otters are dependent on overstory cover ostensibly for shelter and cavities provided by roots of large trees (Bowyer et al. 1995), whereas mink can make use of areas with only abundant understory cover. That the selection of cover by mink did not differ between sites with and without sign of otters suggests that no exclusion occurs on this niche axis. Mink avoided highly exposed beaches even in those sites where otters were unlikely to occur because of sparse overstory cover. This avoidance probably is a result of the swimming and diving capabilities of mink in a marine environment rather than competitive exclusion by river otters; exposed sites have higher prey diversity and biomass (Sousa 1979, McGuinness 1987, Feder and Bryson-Schwafel 1988) and thus should be selected by mink in the absence of otters. Whether mink and river otters hunted the same species and size of prey in those sites in which they both occurred is unclear and merits further investigation. Partitioning of resources could have occurred on other niche axes, because mink also differed from otters in their timing of foraging. Whereas mink foraged mostly during low tide and mainly within the intertidal zone, river otters showed no preference for status of tides (pers. obs.). This might result in differences in availability of prey because intertidal organisms react to tide levels (Feder and Bryson-Schwafel 1988). Additionally, mink are solitary hunters (Dunstone 1993), whereas otters living in marine environments often forage in social groups (Rock et al. 1994). This social foraging might affect diet selection and hunting success. How this difference in sociality affects resource partitioning, however, is unclear.

Powell and Zielinski (1983) suggested that mink and river otters do not compete. They base their conclusion on the difference in body size, difference in diving physiology, and the resource partitioning described in many studies that concentrated on feeding habits of the two species (Erlinge 1972, Melquist et al. 1981, Wise et al. 1981, Humphrey and Zinn 1982). Moreover, differences in body-size correlate with other life-history parameters (i.e., litter size, age at first reproduction) that affect rates of population growth for otters (Dockett et al. 1987) and mink (Linscombe et al. 1982), and likely influence outcomes of competitive interactions. Conversely, Glasser and Price (1988) have shown that both exploitative and interference competition can lead to non-overlapping patterns of resource exploitation (i.e., partitioning). Erlinge (1972) demonstrated that high dietary overlap occurred between mink and otters in Sweden during winter, whereas little overlap occurred in summer. Melquist et al. (1981) determined that although mink and river otters foraged together when food was superabundant, otters left the area when food availability declined. Mink in freshwater as well as in coastal environments may feed on terrestrial mammals and birds (Wise et al. 1981, Dunstone 1993), but in other areas mink concentrate exclusively on fish and aquatic invertebrates (Hatler 1976, Johnson 1985). These observations suggest the possibility of exploitative competition under certain environmental conditions. Several studies reported remains of mink in the faeces or stomachs of river otters (Dunstone 1993), suggesting interference competition. Our study supports Powell and Zielinski's (1983) conclusion; we have documented niche separation, but were unable to attribute it to competition. Moreover, niche separation between these mustelids occurred in an environment where forage was especially abundant (Feder and Jewett 1986, O'Clair and Zimmerman 1986, Rogers et al. 1986). Clearly, abundant prey was not sufficient to prevent niche separation along other niche axes.

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